60. The Peroneal Muscles in Birds. By P. Chalmers Mitchell, M.A., D.Sc., LL.D., F.R.S., F.Z.S., Secretary to the Society.

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(Text-figures 179–190.)

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In the dissection of an example of *Balæniceps rex*, which formed the basis of a recent contribution to the Society's Proceedings (*supra*, pp. 644–703), I was interested to notice that one of the very few characters in muscular anatomy which the Shoe-bill shared with Herons, to the exclusion of Storks, was the presence of the leg muscle known as the Peroneus brevis or profundus. On looking up the literature relating to the peroneal muscles in birds, I found that even Dr. Gadow's careful description of these muscles (Gadow in Bronn's 'Thier-Reich,' Aves, pp. 180–182) was based on a relatively small number of individuals and types, and that his work, together with the insignificant contributions of earlier and later writers, supplied only a vague and dubious picture of the anatomical facts in Aves. I wished to make a survey of these muscles as nearly as possible complete. Accordingly I have dissected them in the birds that have died in the Society's Collection for some months, have made use of the rich spirit material stored in the Prosectorium (most of it dating from the time of Garrod and Forbes), and have been allowed to examine some specimens in the stores of the British Museum (Natural History) and of the Museum of the Royal College of Surgeons, and Dr. Gadow has also obliged me with material from Cambridge. My observations therefore relate to several hundred birds, distributed, as will be seen later, fairly well over the whole Avian system. Theoretically, no doubt, it is necessary to work out the complete anatomical structure of an animal if one would understand any portion of it, but in practice this is impossible, and in my opinion the examination of a single structure or even portion of a structure through the whole series by a single observer cannot fail to be interesting and instructive. The method, moreover, has the practical advantage that the anatomist gains, at least temporarily, a useful dexterity in exposing the structures on which he is engaged and is able to cover much ground in a relatively short space of time.

After giving an account of the muscles in a generalized type, I shall proceed to a systematic description of the conditions presented, following the classification given by Dr. Gadow in the article Bird, in the Eleventh Edition of the Encyclopædia Britannica, and finally shall discuss some of the problems suggested by the degree of coincidence between the varying conditions of these muscles and a classification which is based on other anatomical facts.

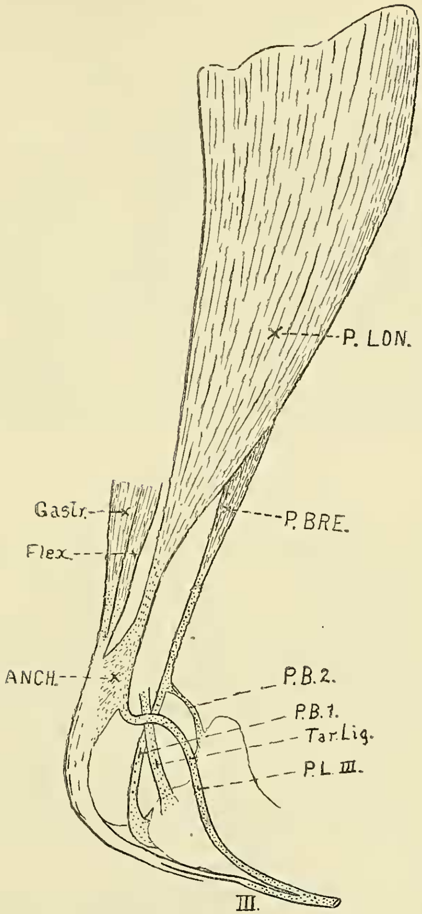
The Peroneal Muscles in Chauna chavaria (text-fig. 179).

In some respects the Screamers are generalized birds with affinities pointing in many directions, and it happens that the condition of the peroneal muscles in other birds can be easily described as specializations of the Screamer condition chiefly by loss of parts.

Peroneus superficialis seu *longus*.—This is the most superficial mass of muscle seen when the skin is removed on the outer, upper aspect of the leg from the knee downwards. Its very large fleshy mass arises from the anterior and lateral crista of the tibia, from the head of the fibula and partly from the fascia covering the knee. Laterally, where it is bounded by the external head of the gastrocnemius on the one side, and the tibialis anticus on the other, its fasciæ are closely attached to the fasciæ of these muscles. The muscular mass is roughly triangular, and from the broad base at its origin from the upper end of the tibia and fibula, it converges to a flat tendon which is apparent about three quarters way down the leg and rather more on the outer than the anterior aspect. There is a deep origin formed by a comb of fibres projecting inwardly as a keel along nearly the whole length of the triangular portion of the muscle and arising partly from the whole length of the fibula and partly from the tibial surface immediately under the fibula. When the tendon has nearly reached the tarsal joint, it gives off a very broad and strong anchor (text-fig. 179, *Anch.*) to the cartilaginous sustentaculum which is pierced by some of the flexor tendons and joined superficially by the gastrocnemius tendon. It is then continued outwards and downwards across the ankle-joint, immediately under the skin, but running through a synovial membrane which has to be cut open to expose it fully, and ultimately, about a quarter of the distance down the tarso-metatarsal shaft, it fuses with the flexor tendon of the third digit (flexor primus seu perforatus III) (text-fig. 179, P.L. III). It is supplied by a branch of the ischiadic nerve.

The function of this muscle is to straighten the tarsus metatarsus on the tibio-tarsus and then to flex the third toe. When

Text-fig. 179.



Peroneal muscles in *Chauna chavaria.*

Right leg, external aspect. Muscle striped : tendon dotted.

P.LON. Peroneus longus. ANCH. "Anchor": attachment of P. longus tendon to Sustentaculum of Flexor tendons. P.L. III. Slip of P. longus tendon passing across the ankle-joint to fuse with III, tendon of Flexor perforatus of the third toe.

P.BRE. Peroneus brevis. P.B. 1. Tendon of insertion of P. brevis passing across the tarsal joint to insertion to proximal end of the tarsus-metatarsus. P.B. 2. Slip of Peroneus brevis tendon, not usually present in birds.

Tar. Lig. Ligament crossing the tarsal joint, deep of P.L. III and superficial to P.B. 1.

Gastr. External head of gastrocnemius muscle.

Flex. Flexor tendons.

the tendon has been dissected out of its synovial groove, it appears too long for its purpose, but if its action be tested before this dissection has been made, it is clear that the straightening of the foot is carried out by the action on the sustentaculum and that subsequently the third toe is bent by the special slip.

The arrangement is odd and very striking, and it is extremely difficult to believe that it has been independently developed in the large number of different groups of birds in which it occurs. In my opinion the disposition of the muscle and its tendons shown in *Chauna* can be explained best if it be regarded as the specialized derivative of a condition in which the perforated flexor muscles and their tendons were continuous with each other and with the peroneus; as the foot and its digits became specialized, the fasciæ of insertion became strengthened along the lines leading to each digit, and finally by the disappearance of the connecting fasciæ the continuous sheet became broken up into separate tendons; as the tibio-tarsus became longer the peroneal slip to the tendon of digit III assumed its odd course. All the stages in the possible differentiation of continuous fasciæ into highly specialized tendons still exist in the case of the alar tendons of birds. The differentiation of the foot, however, must have taken place before the groups of birds became separated, and, as I shall show later, the various conditions of the peroneus in the different groups of birds can all be explained as differentiations of the condition in *Chauna*, in particular by the loss of some part.

Peroneus profundus seu *brevis* (Tibialis posticus of R. W. Shufeldt, " Myology of the Raven," 1870, p. 228).—This is a much simpler and more slender muscle arising fleshy from the fibula and the adjacent surface of the tibia on their anterior aspects, beginning about the level of the insertion of the biceps tendon and extending a little beyond the distal extremity of the fibula, where it passes into a stout rounded tendon (text-fig. 179, P.BRE). The greater portion of the muscle is concealed by the edges of the tibialis anticus and of the superficial peroneal which meet above it. The tendon as it approaches the end of the tibio-tarsus is very close to the bone and is deep of the peroneus longus tendons; it flattens out, runs through a synovial channel, crosses the tarsal joint overlain by a ligament (text-fig. 179, Tar. lig.), which also crosses the joint, and is inserted to the proximal edge of the tibio-tarsus on its posterior, outer aspect (text-fig. 179, P.B. 1). In *Chauna* it also has a second attachment to the antero-median end of the tarsal shaft (text-fig. 179, P.B. 2).

This muscle flexes the tarsus-metatarsus on the tibio-tarsus, and at the same time slightly rotates the foot, depressing the axial, or great toe side, and raising the abaxial, or fourth toe side. The latter action varies with the exact position of the insertion and is often very feeble, as, indeed, is the action of the muscle as a whole.

Systematic Description.

I have found that the following points are the most notable:—

Peroneus longus.—Origin: "superficial," *i. e.* forming a fairly broad external sheet at the proximal end of the tibio-tarsal shaft and arising chiefly from the head of the tibia and fibula and from the fasciæ over the knee-joint; "fascial," from the fasciæ of the tibialis anticus on the one side and from that of the external gastrocnemius and the underlying flexors on the other; "deep," from the side of the fibular shaft and the adjacent area of the tibia on the opposite side from the origin of the peroneus brevis. The "fascial" origin is the least important morphologically and is correlated with the strength and width of the muscle. "Anchor," to the cartilaginous sustentaculum through which the flexor tendons run at the tarsal joint. "Slip to III," the superficial tendon which runs from the peroneus over the tarsal joint to join the perforated flexor tendon of the third toe.

Peroneus profundus.—Origin. Presence or absence of a bony or fibrous bridge at the lower end of the tibio-tarsus. Tendon of insertion.

Relative size of the two muscles.

RATITÆ.

S t r u t h i o n e s. *Struthio.*—The peroneus longus is enormous. Superficial origin extends over to the femoro-fibular ligament and the patella. Fascial origin present. Deep origin represented by a separate head from the lower end of the fibula. Anchor is broad and flat but short. Slip to III strong and rounded. Peroneus brevis absent, but there is a short stout ligament which may represent either the lower portion of the muscle, or, in my opinion, more probably the ligament which crosses the tarsal joint in *Chauna.*

R h e æ. *Rhea americana* (two examples).—P. longus as in *Struthio*, except that the deep origin extends for the greater part of the length of the fibula. P. brevis absent, but tarsal ligament present.

C a s u a r i i. *Casuarius uniappendiculatus.*—P. longus enormous; superficial and fascial origins very extensive, deep origin as in *Rhea.* Anchor short, very wide and partly in slips. Slip to III stout. P. brevis absent but there is a stout tarsal ligament.

Dromæus novæ-hollandiæ.—As in *Casuarius*, but P. longus not quite so large.

A p t e r y g e s. *Apteryx* (? species) (three examples).—P. longus very large; superficial and fascial origins good, but deep origin very slight. Anchor broad and short; slip to III a rounded tendon. P. brevis very much reduced but present as a small flat tendon arising from a few muscular fibres and running in the normal position under the slip to III. This is notably different from the tarsal ligament in the other "struthious birds" and is quite certainly a rudiment of the Peroneus brevis.

In the Ratites the P. longus is the dominant muscle and does not differ except in minor details from the type in *Chauna* which, for convenience, I may call the "normal" arrangement. The Peroneus brevis is at least functionally absent, but the Apteryges stand apart from the others in possessing an undoubted vestige of it.

CARINATÆ.

Colymbomorphæ.

Colymbiformes.

Colymbi. I have not examined a Diver.

Podicipedes. *Podiceps cristata* and *P. minor*.—In both these Grebes the P. longus was badly developed, with delicate superficial and deep origins passing into a long rounded tendon about half-way between the knee and the tarsal joint. In the Crested Grebe this tendon passed straight to the sustentaculum, so that its insertion was represented only by a narrow anchor, there being no slip to III. In the Little Grebe the anchor was similar but I was able to trace a minute but normal slip to III. On the other hand, in the Crested Grebe there was a minute and certainly functionless tendon representing the P. brevis which I did not find in the Little Grebe.

Sphenisciformes.

Sphenisci. *Spheniscus demersus.*—P. longus rather weak but all origins present; anchor and slip to III both slender and short. P. brevis was also slender but arose fleshy from the greater length of the shaft of the fibula and tibia and was inserted by the usual slender flat tendon running in a synovial groove under the slip to III. Gadow mentions that it is present but weak in *Aptenodytes*. Beddard's statement that it does not occur in Penguins is erroneous.

Procellariiformes.

Tubinares.—*Daption capensis. Procellaria* (? species). *Oceanodroma* (? species).—In the Cape Pigeon and the two Petrels the P. longus was rather small with only the superficial origin, which quickly passed into a very long, slender tendon ending in a delicate anchor and a slender slip to III. The P. brevis had a short but strong origin from high up the fibula; this passed into a strong and very long tendon with the usual flat insertion. The P. brevis is rather stronger than the P. longus. The examples of Petrels which I examined were part of the material of W. A. Forbes and had been preserved in spirit for at least thirty years. I was interested to note that they still retained a very strong musky odour, so clinging that although I used several kinds of soap and petrol I could not get rid of it for several days.

It is clear that the Colymbomorphæ present no coherent picture, the Petrels being sharply marked off from the others by the relative dominance of the P. brevis.

Pelargomorphæ.

Ciconiiformes.

Steganopodes.

Phaëthontidæ. *Phaëthon.*—P. longus normal but rather small, with superficial and deep origin, broad anchor and slip to III. P. brevis normal, with long muscular origin and short tendon with usual flattened insertion.

Sulidæ. *Sula bassana.*—P. longus normal and large but with only superficial and slight fascial origin. Broad short anchor and slip to III. P. brevis absent.

Phalacrocoracidæ. *Phalacrocorax* (? species).—P. longus normal and large; origin, anchor and slip to III as in *Sula*. P. brevis strong but very short, arising only from the lower end of the tibial shaft, distal to the fibula, and with normal insertion by flattened tendon.

Fregatidæ. *Fregata.*—Peroneus longus large and strong but origin practically only deep from the whole length of fibula and adjacent surface of tibia on side turned from the brevis. Broad anchor and good slip to III. P. brevis minute but quite distinct and normal, with long slender belly and tendon passing under a fibrous bridge and then flattening out to pass to usual insertion.

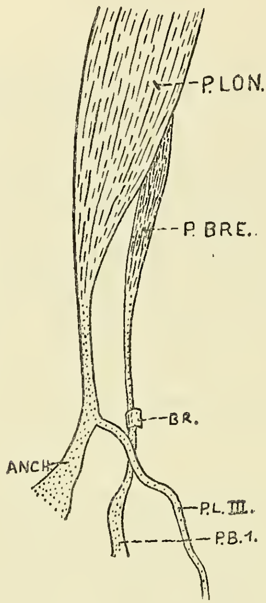
Pelecanidæ. *Pelecanus.*—I have not had a recent opportunity of examining a Pelican, but from my old notes I find that the P. longus is large and normal with the usual anchor and slip to III, and that the P. brevis is present but minute.

Ardeæ (from these I exclude *Scopus* and *Balæniceps*). *Ardea egretta*, *A. herodias*, *A. herodias lessoni*, *A. purpurea*. *Ardetta minuta*. *Nycticorax gardeni*, *N. violaceus* (2 examples). *Botaurus stellaris*, *Cancroma zelodoni.*—In all these the P. longus is fairly large (text-fig. 180), but has only the superficial origin with slight fascial origin. The anchor is rather long, broadens out, and at least in one case (*A. herodias lessoni*) was in two slips. The P. brevis is well developed usually from about three-quarters the length of the shaft but chiefly from the fibula. The long tendon passes through a fibrous bridge and then flattens out to the normal insertion. I think there must be some mistake in Gadow's statement that the P. brevis is absent in *Ardea*. I find that its presence is one of the differences between Herons and Storks. In *Ardetta minuta* and *Cancroma* it is particularly strong.

Scopidæ. *Scopus umbretta.*—The P. longus is large with superficial and slight fascial origin, broad anchor and good slip to III. The P. brevis is either actually absent or represented by a very small ligament.

Balænicipitidæ. *Balæniceps rex.*—P. longus a strong broad muscle with only superficial and fascial origins. Anchor broad and good slip to III. The P. brevis is strong but short, arising only from the tibia distal to the end of the fibula; its flattened tendon passes over to the usual insertion.

Text-fig. 180.



Peroneal muscles in *Nycticorax gardeni*.

Description and lettering as in Text-figure 179 (p. 1041).

Br. Bridge traversed by the tendon of the P. brevis.

Ciconiæ. *Ciconia nigra. Dissura episcopus. Leptoptilus crumeniferus* (2 examples). *Mycteria americana. Pseudotantalus ibis* and *Tantalus loculator*.—In all these Storks the conditions were practically identical. The P. longus was large and strong with superficial and fascial origins and no deep origin, very broad anchor and good slip to III. The P. brevis was absent, but running across the tarsal joint parallel with the slip to III, and therefore approximately at right angles with the normal position of the P. brevis tendon, was a stout elastic ligament which kept the tarsal joint flexed, so that after death the joint could not be straightened without force until this had been cut. At first I thought that this ligament might represent the brevis, but its direction is different, and it does not resemble the indubitable vestiges of the brevis which occur in some other birds.

Ibididæ. *Carphibis spinicollis. Platalea leucorodia. Plegadis falcinellus.*—In these the P. longus is normal with superficial and fascial origins, only a few fibres of deep origin, good broad anchor and slip to III. The P. brevis is present but very weak, arising by a few thin fibres from the greater part of the length of the fibula and passing into a slender but long tendon with the usual flat insertion.

Phœnicopteri. *Phœnicopterus antiquorum.*—In the Flamingo the P. longus is strong with only the superficial and fascial origins, with good wide anchor and slip to III. The P. brevis is absent.

The general picture presented by the Ciconiiformes is of a large well formed longus muscle chiefly with superficial origin, and a brevis muscle almost invariably slender and showing a strong tendency to disappear, but none the less with the presence or absence following the minor divisions of the assemblage, and not being sporadic in the genera.

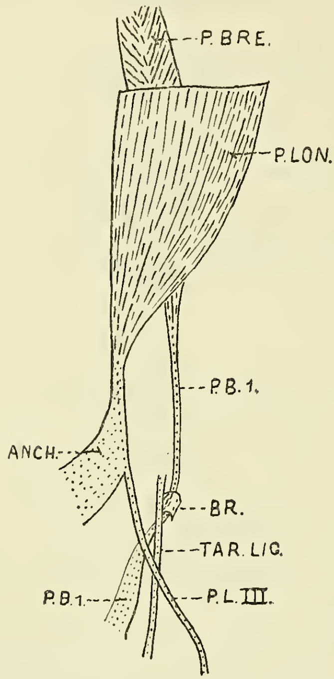
Anseriformes.

Palamedeæ. *Chauna chararia. Palamedea cornuta.*—I have already described the conditions in these (*supra*, p. 1040).

Anseres. *Cygnus olor, C. nigricollis. Æx galericulata* and *Æx sponsa. Cereopsis novæ-hollandiæ. Chloëphaga inornata. Dendrocygna fulva. Querquedula castanea. Metopiana peposaca. Œdemia nigra. Mergus serrator.*—In the Swans, Geese and Ducks the P. longus is large with a very broad superficial origin wrapped round the front of the knee, partly covering and partly with fascial origin from the tibialis anticus and a lesser extension towards the gastrocnemius. The muscle narrows rapidly (text-fig. 181) to a rounded tendon from which a very broad anchor, frequently in separate slips, is given off, the main tendon forming the slip to III. The P. brevis is always present and usually large, with a central tendon and pinnate slips of fibres from the greater part of the fibula and adjacent surface of the tibia. It frequently dips under a fibrous bridge and then flattens out and has an unusually wide insertion to the abaxial side of the end of the tibio-tarsus. There is usually one, and not infrequently a second separate tendon running across the tarsal joint. The variations within the group are small, all the normal parts being present. The deep origin of the longus is usually very slight, but as an exception it is well-marked in *Dendrocygna*. The anchor is very broad and short, and usually in separate slips, but in the ducks generally and in *Dendrocygna* it is rather more fan-shaped. In *Œdemia* the brevis is very short, arising only from the tibia below the fibula and from a small portion of the fibula; its tendon, moreover, instead of crossing under the slip to III runs parallel with it, and is inserted to the axial edge of the tarsus-metatarsus.

In the Anseriformes the peroneals are both well developed, the longus, however, being relatively the larger, but the brevis is actively functional and in addition to its flexion of the tarsal joint has a notable rotating action.

Text-fig. 181.



Peroneal muscles in *Æx sponsa*.

Description and lettering as in Text-figure 179.

The Per. longus has had the proximal portion removed to show the P. brevis.

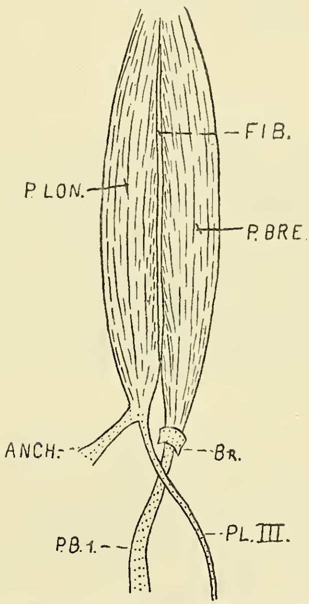
FALCONIFORMES.

C a t h a r t æ. *Cathartes aura* (2 examples).—The P. longus is a strong muscle, with good but rather narrow superficial origin, with fascial origin chiefly on the side of the tibialis anticus, and with extensive deep origin. The anchor is broad and short and the slip to III is very strong. The P. brevis is very slender, arising only from the distal two-thirds of the fibula, then passing into a rounded tendon much weaker than the slip to III under which it runs, and then flattens out to the normal insertion. The dominance of the longus over the brevis recalls the condition in the Ciconiiformes and differs from that present in Accipitrine birds (excluding *Serpentarius*).

Accipitres. Serpentariidæ.—I have had no recent opportunity of examining a Secretary bird, but I infer from Dr. Gadow's statement ("Aves" in Thier-Reich) that both peroneals are present, and that as P. longus is very large the condition is generalized and thus like what exists among the Ciconiiformes.

Vulturidæ and Falconidæ. *Gypaëtus barbatus. Tinnunculus alaudarius. Falco peregrinus* (2 examples). *Aquila verreauxi. Haliaëtus leucogaster. Ictinia mississipiensis. Circus gouldi.*—In all these birds both peroneals are present, but the P. brevis is the more powerful and the P. longus tends to be reduced only to its deep origin. In the Lämmergeier there is the greatest resemblance with the normal arrangement. The P. longus has all

Text-fig. 182.



Peroneal muscles of *Falco peregrinus*.

Description and lettering as in Text-figure 179.

Fib. Anterior edge of fibula.

three origins, but the superficial origin is rather narrow and partly reduced. In all the others the superficial and fascial origins have practically disappeared, so that the muscle, as shown in the case of the Falcon (text-fig. 182), almost exactly balances the P. brevis, arising from the other side of the fibula and the adjacent area of the tibia along the greater part of the length of the shaft. The anchor is always present and is usually rather long and slightly fan-shaped. The slip to III is always present and normal. The P. brevis is very strong: it arises in the Lämmergeier only from the lower end of the fibula and the tibia distal of this; in *Ictinia* its origin begins higher up; in the others, as shown in text-fig. 182, it arises from nearly the whole length of the fibula below the biceps insertion, from the adjacent surface of the tibia and from the tibia distad of the end of the fibula. Its very strong tendon passes under a fibrous bridge which may be calcified in old birds, then flattens out and passes in the usual synovial sheath under the slip to III to its normal insertion.

It is plain that in these birds-of-prey the superficial origin of the P. longus has been partly or completely lost and that the P. brevis has greatly increased in relative importance, until it may surpass the P. longus.

Pandionidæ. *Pandion haliaëtus.*—In the Osprey I found no trace of the P. longus, in which I am confirmed by Dr. Gadow. The P. brevis was short and not very strong, arising from the usual origin limited to the lower half of the shaft and passing into a weak tendon, which after traversing a bony bridge, flattened out and had the normal insertion of this muscle. As ornithologists, arguing from other features, have differed as to placing the Osprey with the Eagles and Vultures, or with the Owls, it is of some interest to note that in the Owls also only the P. brevis is present.

Apart from *Pandion*, it is clear that the Falconiformes generally show a gradual reduction or specialization of the P. longus, always retaining, however, the deep origin, the anchor and a strong normal slip to III, and a gradual increase in size of the P. brevis.

Gadow unites the Ciconiiformes, Anseriformes, and Falconiformes into the "Legion" Pelargomorphæ. Again excepting *Pandion*, it appears that throughout the Legion, the P. longus remains a large and important muscle always with a good anchor and good slip to III, but that the P. brevis offers every condition from that of perfect equality with or even superiority to the longus in the specialized Falcons, to complete absence.

Alectoromorphæ.

Tinamiformes.

Crypturi. *Rhynchotus rufescens* (4 examples). *Nothura maculosa*. *Calodromas elegans* (3 examples).—In all the Tinamus I examined, the P. longus was well developed, with very large superficial and fascial origins and long deep origin. The anchor was strong and broad and the slip to III strong. I noticed that in a Rufous Tinamu the P. longus first straightened the tarsal joint and then flexed sharply the second as well as the third digit. On dissecting out the tendons, I found that the tendon of the perforated flexor muscle of the third digit, after being joined by the tendon from the peroneus, gave off not only the slip to the perforated and perforating flexor of digit III which occurs in birds belonging to many different groups, but also a slip to the perforated flexor tendon of digit II, an arrangement which I have not noted or found recorded in any other bird.

The P. brevis was present in all the Tinamus I examined; in *Rhynchotus* it was very feeble and slender, arising from the greater part of the length of the fibula and passing into a thin tendon which flattened out, and passing under the slip to III had the normal insertion. In *Nothura* its origin was from the lower part of the fibula, and in *Calodromas* it was extremely minute and reduced to a few fibres and a tendon just visible, but running the usual course. The definite presence of the P. brevis in Tinamus is in contrast with its equally definite absence in most of the Struthious birds, but resembles the condition in *Apteryx*.

Galliformes.

Mesitidæ.—I have had no opportunity of examining *Mesites*, and Milne-Edwards does not refer to the peroneal muscles. It would be interesting to know their disposition, as in *Eurypyga* the tendon is characteristically long, and very different from the arrangement in Galliform birds.

Turnices. *Turnix dussumieri.*—The P. longus is present and rather strong, with the three origins, a good anchor and slip to III. The P. brevis is slender but arises from nearly three-quarters of the shaft, from the fibula and tibia, and passes into a short tendon which flattens out to the normal insertion.

Galli.

Megapodiidæ. *Talegalla lathami.*—The P. longus is very strong with large superficial and good fascial origins but no deep origin. Anchor strong but narrow, and good slip to III. The P. brevis is also good, from the posterior three-quarters of the shaft from fibula and tibia. Tendon is very short, passes under a fibrous bridge and then flattens out to pass to usual insertion.

Cracidæ. *Ortalis ruficauda. Mitua tuberosa. Pauxis galeata. Penelope purpurascens.*—In all these the P. longus is enormous but chiefly from superficial and fascial origin, the deep origin being just present. The anchor is very broad, short and strong, and the slip to III is good. In some the tendon was ossified down to the anchor. The P. brevis was strong, arising from the distal three-quarters of the shaft, from the fibula, adjacent surface of tibia and tibia distal to the end of the fibula. The tendon then passed through a long fibrous bridge, partly calcified in *Ortalis*, and flattened out to usual insertion.

Gallidæ. *Guttera cristata*, *G. edouardi*, and *G. pucherani*. *Meleagris gallopavo. Argus giganteus. Gallus gallus* (2 examples).

Calophasis ellioti. Crossoptilon mantchuricum (2 examples). *Rollulus roulroul. Ortyx virginianus* (2 examples). *Lophortyx douglasi. Coturnix coromandelica. Francolinus infuscatus.*—In all these Galline birds the P. longus was enormous, with very strong superficial, well-marked fascial and rather slight deep origins. The anchor was stout and in most cases rather broad and short, but in the Francolin was narrow and rounded. The slip to III was invariably strong. The tendon of the longus was partly ossified down to the anchor in the older birds. The P. brevis was present in all, but in most cases rather slender, and its origin was from the distal three-quarters of the shaft including the fibula, adjacent surface of tibia and tibia distal to the fibula. The rather short tendon (long in one of the Quails) usually passed through a fibrous bridge and then flattened out to normal insertion. In Pucheran's Guinea-fowl, however, the tendon did not pass across the tarsal joint, but ended on a knob on the distal end of the tibio-tarsus in about the position where it occasionally passes through a fibrous or calcified bridge. The P. brevis was relatively weak in all these birds, and the condition in the Guinea-fowl is at least complete functional degeneration, but I have found no case of complete absence, although I examined *Penelope* and *Gallus gallus*, in which Dr. Gadow found it absent.

Opisthocomi. *Opisthocomus cristatus* (2 examples).—The P. longus is of moderate size with only a rather narrow superficial origin. Good anchor and slip to III present. The P. brevis is relatively rather strong, arising from the distal three-quarters of the shaft in the normal fashion and with a short tendon flattening out to the usual insertion.

In the Galliformes the P. longus remains the dominant muscle and is always well developed, with, however, seldom much deep origin. The P. brevis is present but obviously less important.

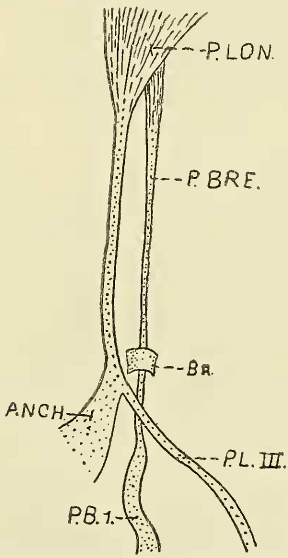
Gruiformes.

Rallidæ. *Fulica leucoptera. Gallinula chloropus* and *G. phœnicura. Tribonyx mortieri. Hydrornia alleni. Porphyrio porphyrio* (2 examples). *Ocydromus australis. Porzana carolina. Aramides chiricote* and *A. ypecaha. Hypotænidia philippensis* (2 examples). *Rallus longirostris, R. maculatus*, and *R. celebensis*.

In all these Rails (text-fig. 183) the P. longus is a strong muscle usually with an extensive superficial and good fascial origin and rather little deep origin. The muscular fibres converge to a powerful tendon, frequently ossified, about the middle of the length of the shaft. The anchor is very strong and tends to be broken into separate slips; the slip to III is always present, with the usual course. The P. brevis is also always present and rather strong, arising from the upper half of the fibula and the adjacent surface of the tibia. It then passes into a stout tendon, sometimes ossified, and having traversed a fibrous or calcified bridge flattens out to the usual insertion. The text-figure, drawn from a Green-backed Porphyrio, gives the arrangement usual in the Family.

Gruidæ. Gruinæ. *Grus australasiana. Anthropoides virgo. Balearica chrysopelargus.*—In the Cranes the P. longus is rather large with extensive superficial, fascial and deep origins, very long tendon sometimes ossified, very wide anchor and good slip to III. The P. brevis is present and arises from nearly the whole length of the fibula but is very weak. The tendon, sometimes ossified, has the usual insertion by a flattened extremity which passes under both the slip to III and a very long tarsal ligament.

Text-fig. 183.



Peroneal muscles of *Porphyrio porphyrio*.

Description and lettering as in Text-figure 179 (p. 1041).

Br. Fibrous bridge.

Araminæ. *Aramus scolopaceus.*—The P. longus is large with superficial and fascial origins but without deep origin. It has a stout anchor and good slip to III. The P. brevis is either altogether absent or represented by a very small ligament.

Psophiinæ. *Psophia crepitans*, *P. leucoptera*, and *P. obscura.*—The P. longus is large with chiefly superficial and fascial origins. The anchor is broad and the slip to III is present and stout, but peculiar in so far as after giving off a stout anchor to the perforated flexor of III in the region where it usually fuses with that, it passes on and joins much more distally the tendon of the perforated and perforating flexor of the same digit. The P. brevis is present, arising from nearly three-quarters of length of the shaft and with usual insertion.

Dicholophidæ. *Cariama cristata* (3 examples).—The P. longus is large with superficial and fascial and slight deep origins and a very long tendon which gives off a very broad anchor and is continued as a slip to III. The P. brevis is represented by a minute muscular head arising from the fibula and tibia opposite the biceps ligament, and a very long slender tendon close to the tibia which after crossing the tarsal joint flattens out to the usual insertion.

Otididæ. *Otis tarda* (2 examples).—The P. longus is very strong with superficial, fascial, and separate deep origins. The tendon is not long and after giving off a broad anchor is continued as the slip to III. The P. brevis was absent.

Rhinochetidæ. *Rhinochetus jubatus*.—The P. longus was very large with all three origins, a stout anchor and good slip to III. The P. brevis was also well developed with an extensive origin along the length of the fibula and adjacent surface of the tibia and had the usual flattened insertion ; it appeared to me to be larger in the Kagu than in any of the other Gruiform birds.

Eurypygidæ. *Eurypyga helias*.—The P. longus was well developed with all three origins, a broad anchor and good slip to III. The P. brevis was also relatively strong, arising from the upper half of the fibula and adjacent tibia and passing into a long tendon which flattened out as it approached the normal insertion.

Heliornithidæ. *Heliornis fulica* seu *Podoa surinamensis* (2 examples). *Podica senegalensis*.—The P. longus was large in all these but with only superficial and slight fascial origins, the deep origin being practically absent. The anchor was very broad and strong, but the usual slip to III, although certainly present, was delicate and could hardly have been functional. The P. brevis was large and strong, with a rounded origin from the proximal portion of the fibula, then a very long tendon partly ossified which passed under a partly calcified bridge to flatten out to the usual insertion.

Of the Gruiform birds the Rails and the Kagu seem to present the most generalized condition of the peroneals since both are present and actively functional, the longus being the dominant muscle. In the Cranes, Seriemas and Bustards, the brevis shows signs of disappearing. The Sun-bitterns and the Finfoots stand apart from the others, the former recalling the condition most frequently found in the Limicolæ, and the latter, with the tendency for the longus to be reduced, being quite peculiar in the group.

CHARADRIIFORMES.

L i m i c o l æ.

Charadriidæ. *Limosa lapponica*. *Actitis hypoleucus*. *Gallinago cœlestis*. *Machetes pugnax*. *Scolopax rusticula* (2 examples).

Himantopus nigricollis. *Recurvirostra avocetta.* *Hæmatopus ostralegus.* *Vanellus vanellus* (3 examples). *Charadrius pluvialis.* *Rhynchæa capensis.*

In all these the P. longus is rather a small muscle with a broad superficial, slight fascial, and very little deep origin from the edge of the fibula. It narrows rapidly to a long tendon which gives off a broad anchor and ends in the usual slip to III. The P. brevis is always reduced, arising only from the proximal part of the fibula and passing into a long slender tendon which passes down the leg parallel with the tendon of the longus, dips under a fibrous bridge at the distal end of the tibio-tarsus, and then passing under the slip to III flattens out to the usual insertion. In the Avocet, two examples of the Lapwing, and in the Oystercatcher, the brevis was reduced to a slender ligament which arose from the distal end of the tibio-tarsal shaft in about the position where it would normally pass through a fibrous bridge, and passed across the tarsal joint to be lost in the fasciæ under the slip to III.

Chionidæ. *Chionis alba.*—The P. longus is present with all three origins, the deep being very feeble. The muscle passes into a very long tendon which has the usual broad anchor and slip to III. The P. brevis is also present but extremely feeble, a few fibres from the fibula passing into a delicate tendon with the usual insertion.

Glareolidæ. *Glareola pratincola* (2 examples).—Precisely as in *Chionis*, the tendon of the feeble P. brevis being still longer and more slender.

Thinocorythidæ. *Thinocorys* ? species.—The P. longus is as in the Glareolidæ and Chionidæ, but the P. brevis is stronger, with an extensive origin from the fibula passing into a long tendon with usual insertion.

Œdicnemidæ. *Œdicnemus scolopax.*—The P. longus is large and strong, with all three insertions passing into a rather shorter tendon with broad anchor and strong slip to III. The P. brevis is represented at most by a vestigial tendon.

Parridæ. *Hydrophasianus chirurgus.* *Phyllopezus africanus.* *Jacana jacana.* *Asarcia variabilis.*—In all these long-toed, long-legged Jaçanas the P. longus is rather large with superficial, fascial, and good deep origins. The broad band of muscle then passes into a very long tendon which gives off a wide but short anchor and is continued as the slip to III. The P. brevis arises from the upper third of the fibula and adjacent tibia and gives rise to a very long tendon which flattens out to the usual insertion.

Lari.

Laridæ. *Larus argentatus*, *L. ridibundus.*—The P. longus has only the superficial origin, and the muscle converges to a very long tendon which gives off a broad anchor and then forms the usual slip to III. The P. brevis arises only from a small proximal portion of the fibula and then forms a very long tendon which runs down the leg parallel with the tendon of the longus, dips under the slip to III, and has the usual flattened insertion.

Alcidæ. *Alca torda*.—The P. longus is fairly large, with superficial and fascial origins, then a long tendon which gives off a broad anchor and ends as the normal slip to III. The P. brevis is also rather strong but much inferior to the longus. It has an extensive origin from the fibula and then passes into the usual tendon with normal insertion.

Pterocles. *Pterocles alchata* (2 examples).—The P. longus is broad and rather strong, with all three origins and broad anchor and slip to III. The P. brevis is absent, so that in this respect the Sand-Grouse agree with the general tendency of the plover-like birds and differ from the game-birds.

Columbæ. *Starnœnas cyanocephala*. *Leucosarcia picata* (2 examples). *Phlogœnas cruentata* and *P. luzonica*. *Geophaps plumifera*. *Phaps chalcoptera* and *P. elegans*. *Columbula picui*. *Geopelia cuneata* and *G. tranquilla*. *Zenaidura carolinensis*. *Carpophaga rufigula*. *Columba livia* (many examples, wild and domestic). *Osmotreron bicincta* (2 examples).

The Doves and Pigeons present an interesting series of modifications. A state of affairs very closely resembling what occurs in Limicolous birds is not infrequent. In *Leucosarcia*, for instance, the P. longus is very strong, with good superficial and fascial origins and a considerable deep origin from the proximal portion of the fibula. The muscular mass narrows to a very long tendon, which eventually gives off a broad anchor and runs on to form a good slip to III. The P. brevis similarly arises chiefly from the proximal portion of the fibula and the adjacent surface of the tibia, passes into a long tendon which after traversing a fibrous bridge flattens out to the usual insertion. The P. longus is definitely the dominant muscle, but the brevis is well formed and functional. In *Columba* the conditions are similar, but the extent of the fibular or deep origin of the longus varies, and the length of the tendon varies inversely with it. In *Carpophaga* the fibular origin of the longus is still more important, and in many of the smaller Pigeons and Doves, and in *Osmotreron*, the deep origin is the more important, the superficial and fascial origins getting weaker; the tendon is shorter, but the whole muscle is relatively feebler. So also in the smaller Doves and Pigeons, the P. brevis tends to degenerate, arising only from the lower end of the fibula and the tibia distad of this, so that the tendon is very short and very different from the typical Limicoline condition. On the other hand, in *Osmotreron*, the P. longus has become smaller and reduced to its deep origin with a relatively short tendon, but the P. brevis has increased in size and is actually stronger than the longus.

In Charadriiform birds generally the P. longus is the dominant muscle and the P. brevis tends to become weaker or to disappear.

In the case of both muscles, the normal arrangement is for the muscular bellies to be limited to the proximal portion of the leg and to give rise to very long tendons. The Pigeons and Doves show the type of the Charadriiform group, but also indications of moving away from it.

In the Alectoromorph group generally, the P. longus remains as the dominant muscle and, except in the aberrant Finfoots, is always large and powerful. The P. brevis varies, sometimes being very feeble or absent, but in some of the Columbæ, as an exception, shows signs of outstripping the P. longus. The great lengthening of the tendons of both muscles in some of the Ralliform and most of the Charadriiform birds may easily be regarded as in correlation with the long legs of these birds. It is interesting to note that the Columbæ show signs of a former long-legged Charadriiform condition.

Coraciomorphæ.

Cuculiformes.

Cuculi.

Cuculidæ. *Cuculus canorus* (2 examples). *Guira piririgua* (2 examples). *Hierococcyx varius.*—In the Guira cuckoo the P. longus is a large muscle with good superficial, fascial, and deep origins. Its tendon gives off a long narrow anchor and then passes on to form the slip to III. In *Hierococcyx* the longus is relatively smaller and the anchor is broader. In *Cuculus* the deep origin is much the most important, and is chiefly from the distal end of the shaft. In all the P. brevis is well developed, with a strong origin from the tibia below the fibula and a varying extension up the fibula. The tendon of insertion runs the usual course under the slip to III, and flattens out to an insertion placed so that the muscle not only flexes the foot but has a considerable power of rotation.

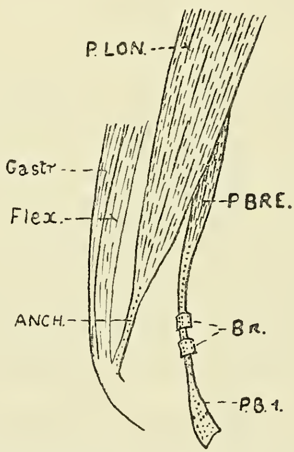
Musophagidæ. *Corythaix persa* (2 examples). *Turacus corythaix.*—The P. longus is a large muscle with extensive superficial and fascial origins and a small deep origin extending down the fibula. The anchor is very broad, and the slip to III well marked. The P. brevis is a long rounded muscle arising from about the distal three-quarters of the length of the shaft, from the fibula and tibia below the fibula. The tendon passes through a fibrous bridge and then flattens out to the usual insertion.

In the Cuculi the P. longus remains the dominant muscle, but there are signs of its being reduced to a deep origin with corresponding increase of the importance of the P. brevis. The group shows, in fact, a transition from the condition which I regard as more generalized towards the particular type of specialization which becomes more and more marked in other Coraciomorphines.

Psittaci. *Stringops habroptilus. Melopsittacus undulatus. Nymphicus uræensis. Nanodes (Lathamus) discolor. Cyanorhamphus alpinus. Platycercus eximius. Aprosmictus cyanopygius. Palæornis fasciata. Eclectus pectoralis* (2 examples), *E. roratus. Pœocephalus meyeri. Caica melanocephala. Pachynus brachyurus. Chrysotis* (? species). *Myopsittacus monachus. Conurus jendayi. Calopsittacus novæ-hollandiæ. Cacatua sulphurea. Trichoglossus novæ-hollandiæ. Lorius domicella.*

Parrots carry further the specialization of the generalized type which is already indicated in the Cuculi. In every case both muscles are present, but there are different degrees to which the longus is reduced and the brevis increased. In *Stringops* (text-fig. 184) the P. longus is a large muscle with good superficial and fascial origins and a deep origin extending nearly the whole length of the shaft. The muscular belly narrows to a short tendon which is inserted to the capsule of the flexor tendons representing what I term the anchor in this memoir. A few

Text-fig. 184.



Peroneal muscles of *Stringops habroptilus.*

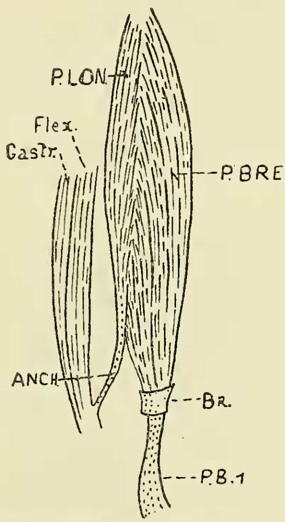
Description and lettering as in Text-figure 179.

Br. Fibrous bridges.

delicate strands can be made out passing in the direction of the usual slip to III, but that structure is certainly absent functionally, even if there be a trace of it morphologically. I have found a small superficial origin of this muscle in several other Parrots; it was relatively large in *Calopsittacus*, and present in *Cyanorhamphus* and *Caica*. Usually, however, it has been lost, and the normal condition in Parrots is for the P. longus to be reduced to a deep origin. This may be large as in *Eclectus*, long but slender as in *Platycercus*, or it may be so small as in

Chrysotis and so closely attached to the fasciæ of the P. brevis that Dr. Gadow has described it as fused with that muscle. I found a minute but distinct slip to III in *Calopsittacus novæ-hollandiæ*, and faint traces of fibres in the direction usually taken by that slip in *Caica*, *Myopsittacus*, and one or two others. The P. brevis in *Stringops* (text-fig. 184) is a stout rounded muscle arising from high up the shaft and passing into a strong rounded tendon, which after traversing two fibrous bridges flattens out to the usual insertion. In most cases, however, it is much stronger than the P. longus, arising from the whole length of the fibula below the biceps insertion, from the adjacent area of the tibia and from the tibia distad of the

Text-fig. 185.



Peroneal muscles of *Platycercus eximius*.

Description and lettering as in Text-figure 179.

Br. Fibrous bridge.

fibula. Its strong tendon usually passes under a fibrous bridge and has the normal flat insertion to the proximal end of the tarsus-metatarsus shaft. *Platycercus* (text-fig. 185) shows the most usual condition of this muscle in Parrots. In *Trichoglossus* and some others the P. brevis is even larger, arising from the head of the fibula proximad of the biceps insertion.

Parrots thus show conditions of the peroneals which link them with the arrangements found in the groups I have already discussed, but as a group are moving away from the normal type in the Coraciomorphine direction.

The Cuculiformes retain marked indications of their former possession of the generalized condition of the peroneals, but have moved away from that condition, the Parrots further than the Cuckoos and Plantain-eaters.

Coraciiformes.

Coraciæ.

Coraciidæ. *Coracias garrula*, *C. indica* (2 examples). *Eurystomus orientalis*.—The P. longus is rather weak, but retains a small superficial, fascial, and slight deep origins. The anchor is very short, and the slip to III is extremely slender but present, at least occasionally. The P. brevis is stronger than the longus; it arises from about the distal three-quarters of the shaft, from the fibula and tibia, passes under a fibrous bridge and is inserted by the normal flat tendon.

Momotidæ. *Momotus lessoni* and *M. subrufescens*. *Aspatha gularis*.—In these the P. longus is well developed with all three origins. It has a short anchor and is continued as a good slip to III. The P. brevis is large and its tendon is just stronger than that of the longus. It arises from the proximal half of the fibula with the adjacent surface of the tibia and gives rise to a rather long, rounded tendon which flattens out at the normal insertion.

Alcedinidæ. *Alcedo ispida* (2 examples), *A. asiatica* and *A. bengalensis*. *Ceryle alcyon*, *C. americana*, *C. inda*, and *C. maxima*. *Ceyx rufidorsa*. *Cittura cyanotis* and *C. sanghirensis*. *Dacelo gigantea* (3 examples). *Halcyon pileata* and *H. rufa*. *Sauropatis chloris*, *S. sancta*, *S. sordida*, and *S. vagans*.—As I have already pointed out in an account of the Anatomy of the Kingfishers ('Ibis,' 1901, p. 97), the P. longus is present in Kingfishers but is plainly degenerating, possibly in association with the degeneration of the fibula. It is best-marked in *Dacelo*; certainly I cannot confirm Beddard's statement ('Structure and Classification of Birds,' p. 199) that it is absent in that bird, and he makes no mention of its presence or absence in other Kingfishers. It has a superficial origin reduced to a narrow tendon from the external corner of the tibial crest, joined by a few fibres from the tibia along the region of the fibula representing the normal deep origin. It is inserted to the capsule of the flexor muscles, this being the usual anchor, but there is no trace of a slip to III. This is the most common condition, but in a few, notably *Ceryle*, *Halcyon*, and *Ceyx*, the muscle is reduced to a simple tendon with only a few muscular fibres, the insertion being the anchor. The P. brevis is always present and strong, arising from the area of the tibia usually covered by the lower end of the fibula and passing into a stout tendon which flattens out to the usual insertion.

Meropidæ. *Merops apiaster*, *M. philippensis*.—The P. longus is present but is very much reduced, having only a narrow superficial and a few fibres of deep origin. A very short anchor is present, and the slip to III although present is very slender.

The P. brevis is much stronger, with a good muscular origin from the distal three-quarters of the shaft; its tendon passes under a fibrous bridge and flattens out to the usual insertion.

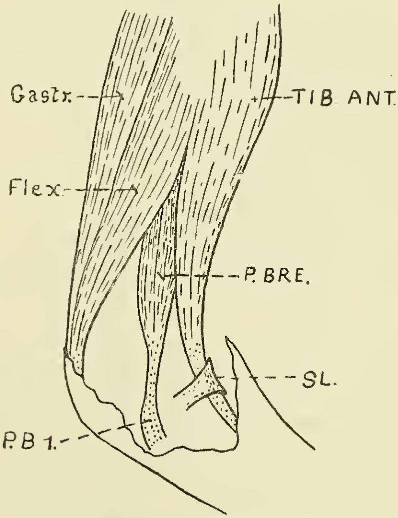
Upupidæ.

Upupinæ. *Upupa epops* (2 examples).—The P. longus is absent. The P. brevis is large, from the distal three-quarters of the shaft, including both fibula and tibia. The tendon flattens out to the normal insertion.

Bucerotinæ. *Bucorvus* (? species). *Rhytidoceros undulatus*. *Lophoceros erythrorhynchus*.—In the Hornbills the P. longus is absent, although I find in my notes that there is a degenerate set of tendinous fibres which might possibly represent a vestige of it. The P. brevis is very strong, arising from the lower half of the shaft, from the fibula and its fibrous continuation, and from the adjacent surface of the tibia. The strong tendon flattens out to form the usual insertion. In *Bucorvus* the P. brevis was equally strong but rather shorter.

Striges. *Athene noctua* (3 examples). *Bubo lacteus* (2 examples), *B. maculosus*, *B. maximus* (2 examples). *Asio otus*.

Text-fig. 186.



Peroneal muscles of *Strix flammea*.

Right leg, outer view. Muscle striped; tendon dotted.

P. BRE. Peroneus brevis. P. B. 1. Tendon of P. brevis.
Gastr. External head of Gastrocnemius.
Flex. Flexor muscle of foot.
Tib. Ant. Tibialis anticus.
Sl. Sling of tibialis anticus.

Strix flammea. Speotyto cunicularia.—There is no trace of the P. longus in any of the Owls. The P. brevis is enormous, but usually arises only from the tibia below the fibula. In *Strix flammea* (text-fig. 186) it is relatively longer, arising from all the fibula distad of the insertion of the biceps, from the adjacent tibial surface, and from the tibia distad of the end of the fibula. In *Athene* it is equally long. The stout tendon flattens out after passing through a fibrous bridge (absent in *Strix*) and is inserted in the normal fashion to the proximal end of the tarsus-metatarsus. Its chief action is to rotate the foot on the tibial shaft so as to depress the great toe side and elevate the fourth digit side. It comes into action after the enormous tibialis anticus has flexed the foot.

Caprimulgi.

Steatornithidæ. *Steatornis caripensis.*—The P. longus is absent. The P. brevis is large and strong, with origin from high up the shaft from both fibula and tibia and fairly long tendon which flattens out to usual insertion.

Podargidæ. *Podargus cuvieri. Nyctidromus albicollis. Ægotheles novæ-hollandiæ.*—In *Podargus* the P. longus has a broad superficial origin with no fascial or deep origin. It gives off a broad anchor and is continued as a slender slip to III. The P. brevis is stronger than the longus. It arises from fibula and tibia just below the insertion of the biceps, and its rounded muscular belly passes into a stout tendon which flattens out to the usual insertion. In *Nyctidromus* the P. longus is practically the same as in *Podargus*, but the P. brevis is absent. In *Ægotheles novæ-hollandiæ* the P. longus is absent, and the P. brevis is well developed, as in *Steatornis*.

Caprimulgidæ. *Caprimulgus europæus.*—The P. longus is large with superficial, fascial, and deep origins. It has a broad anchor and a good slip to III. The P. brevis is absent.

I have followed the usual arrangement of the genera of Caprimulgi that I have examined, and certainly I do not propose to rearrange them simply on the evidence of the peroneal muscles. It is plain, however, that so far as these muscles are concerned, *Podargus* has remained in the primitive condition, with both muscles present and normal; *Steatornis* and *Ægotheles* have specialized in the same direction as the Owls, by losing the P. longus; *Caprimulgus* and *Nyctidromus* present a condition very aberrant amongst Coraciiform birds, and by retaining the P. longus and discarding the P. brevis recall the condition which frequently occurs in the great assemblages which I have already passed in review.

Cypseli.

Cypselidæ. *Cypselus apus.*—The P. longus is absent. The P. brevis is large and strong, from the proximal end of the shaft including the head of the fibula and adjoining area of the tibia down three-quarters of the shaft, then a very strong tendon passing over the bridge of the tibialis anticus to usual flat insertion.

Trochilidæ. *Amazilia feliciæ*.—The P. longus was absent and the P. brevis exactly as in the Swift.

Colii. *Colius capensis*.—The P. longus was present in a vestigial condition, with only superficial origin and a slender tendon ending in the anchor, with no slip to III. The P. brevis was very large and strong, arising from nearly the whole length of the shaft, involving both fibula and tibia. Its strong but rather short tendon flattened out to the usual insertion.

Trogones. *Trogon puella* and *T. atricollis*.—The P. longus was present but not so large as the P. brevis; its origin is chiefly deep, and it has a broad anchor and fair slip to III. The P. brevis is very large and strong, arising from the greater part of the length of the shaft and ending in a short but stout tendon which flattens out to the usual insertion.

Pici.

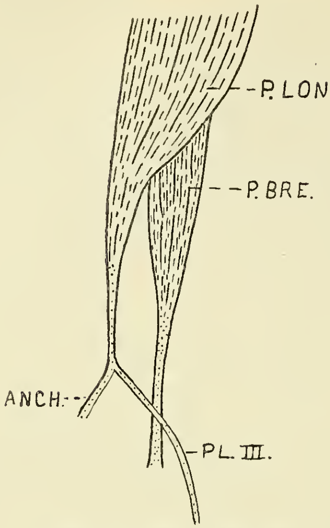
Galbulidæ. *Galbula albirostris, G. rufiventris. Urogalba paradisea*.—My material for examining these was not good, consisting of partly dissected specimens which had been in spirit for many years. The P. longus was certainly very small, but there was a distinct tendon running to form an anchor, and in one case a trace of the slip to III. The P. brevis was larger than the longus and had a stout tendon flattening out to the usual insertion. I should be glad, however, to examine fresh specimens.

Capitonidæ. *Megalæma virens. Cyanops flavifrons*. — The P. longus was a large muscle with a wide superficial, and short fascial and deep origins. The triangular muscular belly rapidly narrowed to a stout tendon, which, however, was not so strong as the tendon of the brevis, gave off a long and rather narrow anchor and was continued as a good slip to III. The P. brevis arose from the fibula beginning just below the biceps tendon, and from a considerable part of the tibia, and passed into a strong tendon which flattened out to the usual insertion. (Text-fig. 187.)

Rhamphastidæ. *Aulacorhamphus prasinus. Pteroglossus inscriptus. Rhamphastos discolor* (2 examples). *Selenidera maculirostris* (2 examples).—In all these Toucans (text-fig. 188) the P. longus was of fair size but with chiefly fascial and long deep origins. The short tendon gave off a narrow anchor and was continued as a slender slip to III. The P. brevis was a stronger muscle, its stout tendon forming the axis of a muscular mass arising from the tibia and fibula for three-quarters the length of the shaft. The tendon then passed through a strong fibrous bridge and had the normal flat insertion.

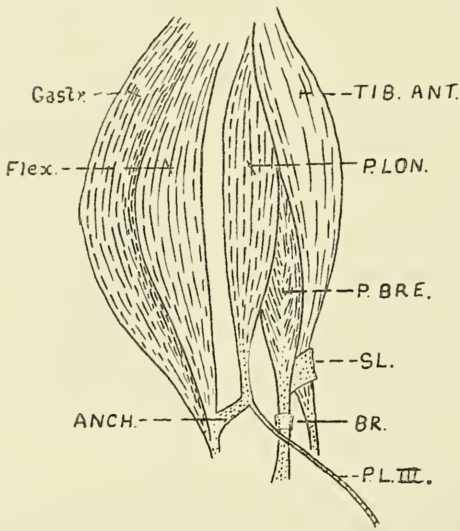
Picidæ. *Dendrocopus major. Brachypternus aurantiacus. Colaptes mexicanoides. Gecinus vittatus. Hypoxanthus rivolii*.—In the Woodpeckers I found the P. longus always present but rather weak and with chiefly superficial origin. Its tendon was very thin and flat and formed the usual anchor, and gave off a thin

Text-fig. 187.



Peroneal muscles of *Megalæma virens*.
Right leg, outer view. Muscle striped; tendon dotted.
P. LON. Peroneus longus. ANCH. Anchor to Sustentaculum. PL. III. Slip to Flexor of III toe. P. BRE. Peroneus brevis.

Text-fig. 188.



Peroneal muscles of *Rhamphastos discolor*.
Description and lettering as in Text-figure 186 (p. 1061).
P. LON. Peroneus longus. ANCH. Anchor. P. L. III. Slip to III.

strand which in a fresh example of *Dendrocopus* formed the usual slip to III, but which in the other Woodpeckers, of which I had only very old spirit specimens, I could not trace completely to their insertion. The P. brevis was strong, arising from the distal three-quarters of the shaft, and ending in a short tendon which flattened out to the usual insertion.

The Coraciiform birds form an interesting and difficult series, but it is clear that the general tendency in the group is for the P. brevis to increase and for the P. longus to be reduced. The series, however, is not very coherent. A certain number have remained almost in the generalized condition with the P. longus possibly slightly reduced in its origin and equal to or weaker than the P. brevis, but showing the anchor and slip to III, and with the P. brevis a strong but not excessively strong muscle. These central types are the Coraciæ, Momotidæ, Meropidæ, *Podargus* amongst the Caprimulgi, and the Trogones, Capitonidæ, and Rhamphastidæ. In others the P. longus is still further reduced and has lost the slip to III, whilst the P. brevis has relatively still further increased. These are the Alcedinidæ (Dr. Gadow, however, states that *Pelargopsis* has proceeded still further to the complete loss of the P. longus), the Colii, the Galbulidæ (probably), and most of the Picidæ. In yet another set the specialization has proceeded to the complete loss of the P. longus, and the P. brevis is always very strong. These are the Bucerotidæ, Upupidæ, Striges, and, amongst the Caprimulgi, *Steatornis* and *Ægotheles*, the Cypselidæ and the Trochilidæ. Finally, in *Nyctidromus* and *Caprimulgus*, although the P. longus is partly reduced, the P. brevis is absent.

PASSERIFORMES.

Passeres Anisomyodæ.

Subclamatores. *Eurylæmus ochromelas*. *Cymbirhynchus macrorhynchus*.

Clamatores. *Picolaptes affinis*. *Chasmorhynchus nudicollis*. *Tyrannus melancholicus*. *Myiarchus tyrannulus*. *Pitangus sulfuratus*. *Pitta strepitans*.

Passeres Diacromyodæ.

Suboscines. *Menura superba*.

Oscines :—

Corvidæ. *Cracticus destructor*. *Creadion carunculatus*. *Cyanocorax luxuosus*.

Paradiseidæ. *Parotia lawesii*. *Ælurœdus melanocephalus*.

Sturnidæ. *Enodes erythrophrys*. *Mimo dumonti*. *Acridotheres fuscus*.

Icteridæ. *Icterus jamaicai*. *Ostinops decumanus*.

Ploceidæ. *Estrelda phœnicotis*.

Tanagridæ. *Tanagra sayaca*. *Rhamphocœlus brasilius*.

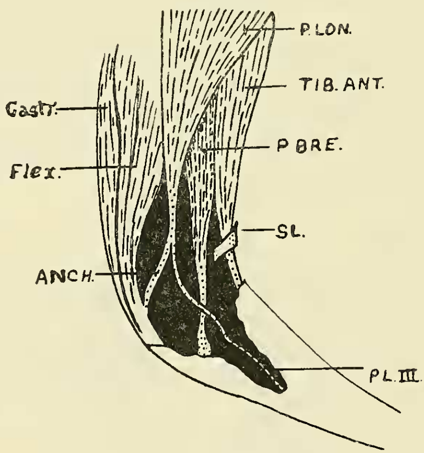
Cœrebidæ. *Cœreba cyanea*.

Meliphagidæ. *Entomyza cyanotus*. *Acanthorhynchus* (2 species).

Nectariniidæ. *Arachnechthra zeylonica.*
Troglodytidæ. *Campylorhynchus unicolor.*
Hirundinidæ. *Hirundo rustica.*
Laniidæ. *Lanius excubitor.*
Artamidæ. *Artamus leucogaster.*
Dicruridæ. *Dicrurus* (? species).
Oriolidæ. *Oriolus galbula.*
Parridæ. *Liothrix luteus.*
Turdidæ. *Turdus tristis. Merula tamaulipensis. Geocichla citrina. Mimus orpheus.*

The Passeriform birds that I examined were well distributed over the divisions into which systematists have attempted to divide this group, and presented a fair sample of the manifold types of habit and size that occur in the group, a sample that I take to be fairly representative, as I found extremely little divergence. The type which recurs throughout the group with a uniformity that is almost tiresome, is well shown in the figure of *Parotia lawesii* (text-fig. 189). Both peroneals are present, well

Text-fig. 189.



Peroneal muscles of *Parotia lawesii.*
Description and lettering as in Text-fig. 188 (p. 1064).

developed and functional. The longus has a broad superficial, good fascial, and fairly long deep origins; the muscular mass is an elongated triangle which ends in a short tendon which almost at once forks, the shorter and stouter fork forming a long narrow anchor, the other forming the "slip" to III. This "V"-shaped forking is very different in appearance from the broad and short anchor which is the more common type in other groups, but it occurs also in other birds and can be regarded only as typically not characteristically passerine. The P. brevis arises from the fibula below the insertion of the biceps tendon and from the adjacent surface of the tibia; the fusiform belly gives rise to a short tendon which frequently, but not invariably, traverses a fibrous bridge and then flattens out to the normal insertion to the proximal end of the tarsus-metatarsus.

The minor differences which are to be found, but too irregularly to be correlated with size, habit, or systematic position, relate to the relative sizes of the two muscles. Sometimes the P. longus is rather feebler with little deep origin and a relatively narrow superficial origin; the P. brevis, on the other hand, becoming very thick and strong. The muscular bellies of both muscles may be shorter and their tendons longer.

In only two of the Passeriform birds examined did I find notable differences. In *Menura superba*, the inclusion of which amongst the Passeriformes I doubt on other grounds, the anchor of the P. longus was much shorter and rather wider than usually occurs in the group, and the P. brevis was relatively considerably weaker. In *Hirundo rustica* the P. longus had the usual broad superficial origin but very little deep or fascial origin, and the slip to III was absent. The P. brevis was of the usual Passerine type and relatively weaker than in the Swifts.

The Coraciomorphine birds present many different phases of the degeneration of the longus and of the increasing importance of the brevis, and in this respect are in marked contrast with the other Legions into which Dr. Gadow has arranged the Orders of birds.

Summary and Conclusions.

The Peroneus longus muscle shows every gradation from elaborate structure and apparently important function to complete absence, and the facts fall into a coherent picture if we suppose that we have to deal with loss of parts originally present. The presence and absence of origin from the fasciæ of the neighbouring muscles are the most irregular and may well be interpreted as in direct relation to function. If the muscle be large and important, it overgrows its bounds and comes in organic contact with the adjacent fasciæ; if it is smaller and less important it remains isolated. When the muscle as a whole appears to be in process of degeneration, this may proceed in two ways. Occasionally, but rarely, the deep origin begins to disappear first, and the superficial origin gradually narrows until it becomes only a thin superficial tendon. More often the process starts with the degeneration of the superficial origin, and this is often accompanied by strengthening and lengthening of the deep origin, until finally nothing but the deep origin is left. This next gradually shortens until the whole muscle disappears. Of the tendons of insertion, the slip to III goes first and the anchor persists. There are many cases in which the slip to III has been lost, the anchor remaining as the only insertion, but I have found no instance in which the anchor has disappeared leaving only the slip to III. The pull on the anchor by the contraction of the muscle not only straightens the tarsal joint, but steadies the sustentaculum and therefore assists the action of all the flexors of the toes; the slip to III acts merely as an accessory to the proper flexor of the third toe.

I find the Peroneus brevis very difficult to understand. Its rotating action is often extremely slight, and in its action in flexing the tarsal joint it appears to do little more than assist the much more powerful tibialis anticus, the mechanical arrangement of which is more favourable. So far from it being surprising to find that it has degenerated or completely disappeared in so many groups, it is remarkable that it should have been preserved at all. In the cases in which it has become stronger and has surpassed the longus, it seems to me that its power of rotation is greater, and in a number of cases, particularly in Passerines, its contraction appears to have the effect of partly flexing the toes and the great toe, as if its action would assist in perching. I am afraid, however, that an equally elaborate investigation of all the muscles of the lower leg would be necessary before the varying conditions of the peroneals could be interpreted in terms of function.

On the information at my disposal I find it extremely difficult to associate the conditions of the peroneal muscles with differences in habit that point directly to functional adaptation. On the other hand, with a few, a very few, exceptions to which I shall refer later, there is a close conformity between the condition of the peroneals and what appear to be the most securely founded systematic divisions. Birds seem to have this or that type of peroneal muscle, not because they are arboreal or terrestrial, swimmers or waders, scratchers, predatory or vegetarian, but because it is the type occurring in this or that systematic division. Whatever be their habit they seem to make shift with the type of peroneal which occurs in their group. All the four Legions into which Dr. Gadow groups the Orders of Carinate birds, and most of the orders themselves, show certain members with what I have assumed in this paper to be the generalized, possibly the more ancestral condition of the peroneals, and all show signs of moving in a definite direction away from this generalized condition. In the Ratites the longus is dominant but the group has moved away from the central type by extreme reduction or total loss of the brevis. Of the Colymbomorphæ the Penguins show the central type, the Grebes have a weak longus with the slip to III occasionally absent, but the brevis is always rudimentary or absent. In the Petrels the longus has always at least a superficial origin, the anchor and slip to III, but the brevis has relatively increased in size. In the Pelargomorphæ (except *Pandion*), the longus remains the dominant muscle and always has both the anchor and the slip to III, and the brevis, except in the Falconiformes, tends to disappear. Some Steganopods, Herons and Ibises, Screamers, and Ducks and Geese remain in the central position. Other Steganopods and Storks and Flamingos have lost the brevis altogether. The Falconiformes show an interesting series. *Serpentarius* is in quite the central position; in *Cathartæ* the superficial origin of the longus is slightly reduced, but the muscle remains the dominant of the pair. In the Falconidæ (omitting *Pandion*) the superficial origin and the longus generally tend to be reduced, but the anchor and slip to III always persist and are strong and functional; the brevis increases greatly and may equal or surpass the longus. In so far the Falconiformes present a parallel with the Owls, but are to be distinguished from that group by the retention of the longus with its anchor and slip. In the Alectoromorph Legion the great majority remain in the central condition. The longus is invariably present, the superficial origin is almost invariably the stronger, the anchor is always present and the slip to III absent only in the Heliornithidæ. The brevis is almost invariably the weaker muscle and shows a strong tendency to disappear, *e. g.* among the Tinamus it may be excessively feeble, it is feeble or degenerate in some Galliform birds, absent or reduced in some Gruidæ and some Charadriidæ. The Columbæ are specially interesting; the longus is always present with anchor and slip to III, but there seems to be a tendency for it to be reduced and for the brevis to increase, especially in the smaller and most Passerine-like Pigeons.

In the Coraciomorphine Legion the characteristic tendency is for the reduction of the longus at the expense of the brevis. The Orders, however, show marked differences in the extent to which this process has occurred. Of the Cuculiformes, the Cuckoos and Plantain-eaters remain almost in the central condition, and, although the brevis is always well developed, it is surpassed by the longus. The Parrots, like the Pigeons, show within the group all stages from an almost central condition where the longus is complete and surpasses the brevis, through stages in which the longus is still well developed, although it has lost the slip to III, to the final stage in which there is almost no trace of the longus remaining. The Coraciiformes have moved furthest from the central condition. A very few, the Motmots, some of the Kingfishers, *Podargus* among the Caprimulgi, and Trogons and Barbets show almost the central condition, but even amongst them the longus is usually very little superior to the brevis, although it retains its parts. In most Coraciiformes the longus is at least feeble, has usually lost its slip to III and is often entirely absent. The Passeriformes, on the other hand, are remarkably constant and very near the central condition, although the brevis may equal or nearly surpass the longus, and in one case (*Hirundo*) the slip to III has been lost. In the diagram reproduced as text-fig. 190, I have endeavoured to show in a diagrammatic fashion the general trend of the modification of the peroneals in the groups of birds. The central space represents the central or primitive condition, the area to the left the degeneration of the brevis, that to the right the degeneration of the longus. The placing of the named enclosures represents roughly the position of the different groups with regard to the central avian condition. It is to be noted that nearly every group seems to have made experiments in both directions, but as we read from above downwards in the diagram, we pass from movement towards the left to movement towards the right. And it may also be noticed that, in a general way, what are usually regarded as the groups exhibiting the lower modifications of avian structure are towards the top of the diagram, those representing the higher types towards the bottom. If I had felt justified in expanding this diagram, by placing the names of the minor groups in their proper orientation with regard to the peroneals, it would have been found in the same fashion, that inside each group, on the whole, those which are generally regarded as the higher types were towards the right hand side of the spaces, those representing the lower types towards the left hand. In other words, I think I may say that the higher types of avian modification are associated with a tendency for the degeneration of the Peroneus longus and an increase of the Peroneus brevis.

Adaptation, direct or associated, may be the fundamental explanation of the facts that I have tried to set out, but it is difficult to follow, and it is easy to see that kinship appears to be a more important factor. The Eagles and Vultures have many adaptive resemblances with the Owls, but the former contain members directly linking them with the primitive condition and have never moved far from it, and the latter show the extreme modification of the Coraciiform group. Swifts and Swallows have many points in common, but the former, in the condition of the peroneals, are extreme Coraciiform birds, the latter very slightly modified from the true Passerine condition. So also Humming-birds are extreme Coraciiformes in this respect, and Sun-birds are true Passerines. The family tradition appears even in many of the minor changes; all the Storks have lost the brevis and the Herons have retained it.

There remains to say a word as to the few birds which do not lie comfortably, so far as the peroneals are concerned, in the positions usually assigned them. In a memoir dealing with a similar large series of facts in bird anatomy ("On the Intestinal Tract of Birds," Trans. Linn. Soc., Zool. viii. p. 173), I pointed out what seems a logical necessity (frequently, however, overlooked by those who use anatomical characters for systematic purposes), that if we have reason to believe a particular character to have been ancestral, we cannot assume that animals now without it are more nearly allied than those that have retained it. There is no *a priori* ground for assuming that it may not have been lost twice or several times independently. It follows therefore that the loss of the longus muscle, or of any important part of it, or of the brevis muscle, is no valid clue to systematic position.

It is equally clear that the common retention of the ancestral condition is no ground for placing the descendants of a particular ancestral stock together, if relative affinity and not convenience is to be the basis of classification.

A glance at the table (text-fig. 190) will show why anatomists on the hunt for convenient systematic characters would take

Text-fig. 190.

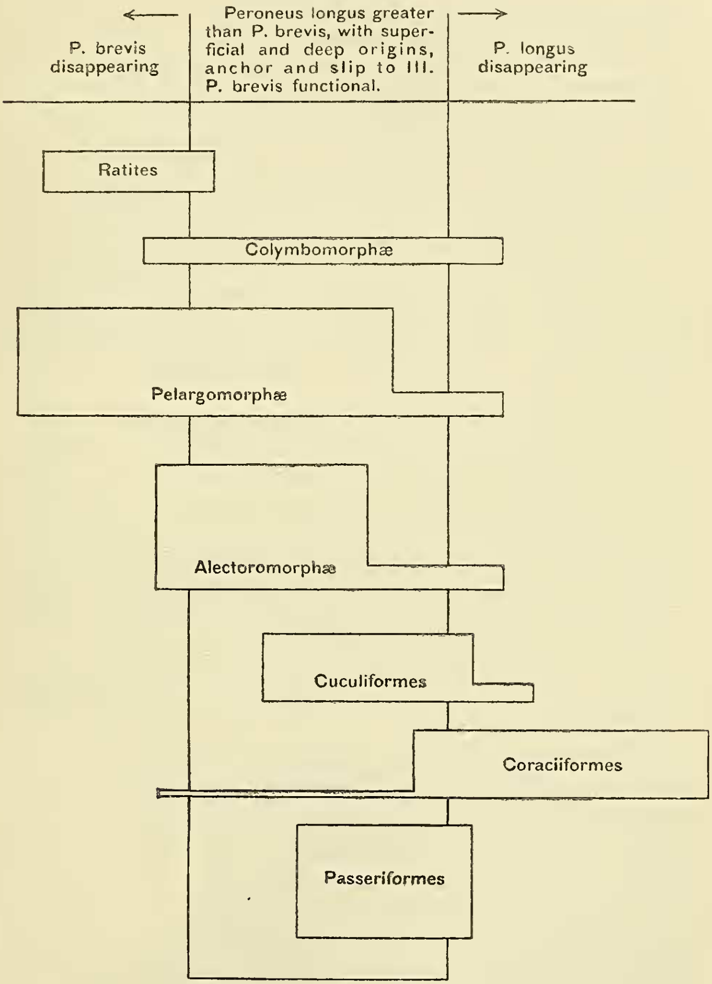


Diagram of Peroneal muscles in Birds.

The central space represents the condition regarded as primitive in this memoir, the P. longus being fully developed, with superficial and deep origins, anchor and slip to III, and stronger than the P. brevis, which, however, is present and functional. The various enclosures represent the groups of birds indicated by the lettering. Coincidence with the central space indicates that the primitive condition of the peroneals is present: displacement towards the left indicates reduction of the P. brevis, displacement to the right reduction of the P. longus.

little interest in the peroneals. Some of the Colymbomorphs, most of the Pelargomorphs, most of the Alectoromorphs, most of the Cuculiformes, a few Coraciiformes, and most of the Passeriformes would have to be placed together. We know from other reasons that the association would be absurd, but it is not more illogical than to place *Ornithorhynchus* and *Echidna* in the same Order because they have retained a reptilian legacy that was probably once the common property of all mammals. The Ratites, some of the Colymbomorphs, some of the Pelargomorphs, and a few of the Alectoromorphs would have to be placed together because of the absence of the brevis. Some of the Colymbomorphs, and a few Pelargomorphs, a few Alectoromorphs, a few Cuculiformes, most of the Coraciiformes, would similarly have to be placed together because of their loss of the longus. A rather tedious piece of work may be of some use, if only it serve to direct attention to the confusion that must arise if characters be not carefully analysed before they are employed for systematic purposes, and to the information which apparently unruly facts may afford, if they are plotted out over a sufficiently comprehensive field.

On the other hand, although the common retention and common loss of ancestral character are no proof of affinity, I myself, like most anatomists who have taken an interest in trying to correlate their facts, have been impressed by the fashion in which allied animals march along the path of modification in the same direction. I have found this to be the case in Pigeons (Journ. Linn. Soc., Zool. xxvii. p. 210), in Kingfishers ('Ibis,' 1901, p. 97), in Gruiform birds (P. Z. S. 1901, p. 629), and in Limicoline birds (P. Z. S. 1905, p. 155), and the general results which I have been stating in this communication point in the same direction. It appears to me therefore that the existence of notable unconformity at least suggests that the position assigned in the System calls for enquiry.

The first notable instance is *Pandion*, which in the matter of the peroneals differs from all the Eagles and Vultures and conforms with the Owls. I cannot find that this point in its structure has been recorded previously, but many systematists have seen in *Pandion* a link between the nocturnal and diurnal birds of prey, and others have actually placed it amongst the Owls. The question calls for re-examination.

I am less impressed with the cases of *Nyctidromus* and *Caprimulgus*. So far as the longus is concerned they agree closely with *Podargus*, but although the latter, like all other Coraciomorphine birds, has a well-developed brevis, the two former have no brevis. I have already pointed out that at the best the action of the brevis is difficult to understand, and appears to be frequently superfluous. I am therefore of the opinion that its loss in these isolated cases, however curious, is insignificant.